

Cosmopolitan Earthworms— A Global and Historical Perspective

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14.1 INTRODUCTION

Apart from their manifest ecological importance, megadrile oligochaetes—the so-called “common earthworms”—are of particular phylogenetic and biogeographical interest since they are an ancient and diverse group with generally feeble powers of overland travel so that most are confined to their areas of origin. Sims (1980) said the slow-moving Oligochaeta could be regarded as excellent subjects for zoogeographical studies were it not for the paucity of fossil records for these soft-bodied animals. Conversely, due to their antiquity and relative stability in soil, those that persist today, especially in primitive families, are more akin to “living fossils.” Thus, the main obstacle to studying their zoogeography is the lack of comprehensive ecological and taxonomic surveys for most regions.

Precursors to earthworms possibly emerged in the late Precambrian some 650–570 million years ago (Valentine 1980), or in the Proterozoic one billion years BP (years before present) (Seilacher et al. 1998). Classified as ecosystem engineers or “bioneers” in the colonization and preparation of soil, these ancestral forms predate the invasion of land by plants, fungi, insects (400–500 million years BP) and occur well before others with similar descent to these early worms, such as reptiles or mammals (200 million years BP), arose (Launer 2006). Earthworms are ubiquitous in all but the driest and coldest regions, and present-day global distributions of the 20 earthworm families have been used to validate Wegener’s hypothesis of continental drift and theories of plate tectonics (e.g. Wegener 1915; Michaelsen 1922; Sims and Easton 1972; Sims 1980; Lee 1981, 1985, 1994).

Only recently have some species with common family ancestries, separated over geological time by the drifting continents, been reunited due to unintentional and sometimes deliberate transportation, literally following in the tracks of human endeavors, particularly those involving agriculture, trade and commerce rather than by natural means. Schwert and Dance (1979) netted lumbricid cocoons from Canadian streams, but there are few actual observations of natural dispersal (cf. Schwert 1990); thus, we can

only assume these modes of transportation from outcomes such as the relatively wide distribution of native *Heteropodrilus* in Australia corresponding with (present and past) catchments of the Murray–Darling river system (Blakemore 2000b, 2006b). And while no earthworm genus is known to naturally transcend wide oceanic barriers, some exception may be found in those few genera with euryhaline species (saltwater tolerant as adults and/or cocoons) or in those that obtain assistance by rafting on flotsam (e.g. in soil within tree root boluses) or carriage in mud adhering to feet of birds. Thus, Michaelsen (1905) thought it likely that *Microscolex* originated in South America and its circum-Antarctic distribution was largely due to rafting on prevailing West Wind Drift in the last few thousand years. Examples of euryhaline species are found in genera *Diachaeta*, *Eukerria*, *Microscolex*, *Pontodrilus* and—from Sims (1980) and Blakemore (1999)—*Pontoscolex*, but many of these are also thought to have had their ranges extended considerably by human-mediated transportation. Two of the most widely distributed species are *Pontoscolex corethrurus* (Müller 1856) and *Pontodrilus litoralis* (Grube 1855); the latter, found on tropical beaches around the world and probably originating from the Indo-Australasia region, was likely spread initially as a ships' beach-sand "ballast waif" and secondarily by its cocoons rafting on flotsam (Subba Rao and Ganapati 1974; Blakemore 2007a).

In general, the degree of regional endemism depends on palaeogeological history and the extent of glaciation and/or volcanism, whereas present-day distribution of the relatively few exotics is strongly influenced by recent, historic and prehistoric human trade and migrations (Stephenson 1930; Gates 1972; Lee 1985, 1987; Sims and Gerard 1985; Blakemore 2002, 2005, 2006a). Accordingly, an earthworm population potentially comprises four components (Blakemore 1999): *resident natives* that are often highly endemic; *introduced exotics* that tend to be more widespread; *translocated natives*, i.e. endemic species that have been transported or redistributed outside their natural range within a bioregion; and *neoendemics*, i.e. members of nonnative genera that have sojourned for sufficient time following their introduction to have undergone speciation in a new region (or are currently unknown or extinct in their places of origin).

Examples of neoendemics may be the *Dichogaster* species (Octochaetidae from Africa) that Stephenson (1931) thought diversified on the Pacific Isles, and several *Microscolex* species (Acanthodrilidae from South America) apparently found uniquely on sub-Antarctic islands. In Europe, Sims and Gerard (1985, 1999) said, "Most British species are allochthonous [= exogenous or non-native, cf. autochthonous] of the remaining half-a-dozen we can only speculate how they came to occupy these lands and whether more remain to be discovered"—although to which taxa they refer is unclear as all their lumbricids are common cosmopolitans. Australia's neoendemic species are exemplified by *Rhododrilus* (Acanthodrilidae from New Zealand) and *Begemius* (Megascolecidae from Papua New Guinea), both having several taxa in northern Queensland; also *Microscolex macquariensis* (Beddard 1896), which is confined to Macquarie Island, and *Microscolex kerguelarum* (Grube 1877) on Kerguelen and Heard Island in the Southern Ocean. The long-anticipated "missing link" of native Octochaetidae in Australia, intermediate between those in India and New Zealand, was recently determined, viz *Octochaetus ambrosensis* (Blakemore 1997), yet no claim is made that some other taxa now found in Australia, such as the circumundane *Microscolex dubius* (Fletcher 1886) from South America, nor *Octochaetona beatrix* (Beddard 1902) from India, are neoendemic; rather, these qualify as cosmopolitan species (Table 14.1).

Cosmopolitan species, the main consideration here, are those species both exotic to a region and widespread due to transportation mainly via human activities. Whereas the

Table 14.1 Nonendemic species in Pacific compared to North American and Indian Ocean regions (family classification after Blakemore 2000)

Families (origins) and Species from Regions	Mainland Australia (excluding Tasmania)	Tasmania	N.Z.	Japan (excluding Ryukus)	Ryukyu Islands	Korea (including Cheju Island)	Taiwan	China (including Hainan)	SE Asia	USA and Canada	Mexico	Hawaii	P.I.	India and Sri Lanka	Myanmar (Burma)
Moniligastridae (India and Oriental)															
<i>Desmogaster sinensis</i> Gates 1930								+							
<i>Drawida barwelli</i> (Beddard 1886)	*							* ^(H)	+		+				+
<i>Drawida japonica</i> (Michaelsen 1892)				+		+	+	+	+						
<i>Drawida longatria longatria</i> Gates 1925									+						+
<i>Drawida nepalensis</i> Michaelsen 1907								+	+						+
Glossoscolecidae (Neotropical)															
<i>Pontoscolex corethrurus</i> (Müller 1856)	++ ^(CI)		+	+	^(BI)	*	+	+	+	+	+	+	+	+	+
Almidae (Tropics)															
<i>Glyphidrilus papillatus</i> (Rosa 1890)								+	^(HI) ?					+	+
Hornogastridae (Mediterranean)															
<i>Hornogaster redii</i> Rosa 1887										+					
Criodrilidae (S-W Palaearctic)															
<i>Criodrilus lacuum</i> Hoffmeister 1845										+				+	
Sparganophilidae (Nearctic)															
<i>Sparganophilidae tamesis</i> Benham 1892											+				
Lumbricidae (Holarctic)															
<i>Allolobophora chlorotica</i> (Savigny, 1826)	+	+	+							+	+				
<i>Allolobophoridella eiseni</i> (Levensen, 1884)		*	+							+		+		+	
<i>Aporrectodea caliginosa</i> (Savigny 1826)	+	+	+	+		+	+	+		+	+	+	+	+	
<i>Aporrectodea icterica</i> (Savigny 1826)										+					

(Continued)

Table 14.1 (Continued)

Families (origins) and Species from Regions	Mainland Australia (excluding Tasmania)	Tasmania	N.Z.	Japan (excluding Ryukus)	Ryukyu Islands	Korea (including Cheju Island)	Taiwan	China (including Hainan)	SE Asia	USA and Canada	Mexico	Hawaii	P.I.	India and Sri Lanka	Myanmar (Burma)
<i>Aporrectodea limicola</i> (Michaelsen 1890)	B+									+		+			
<i>Aporrectodea longa</i> (Ude 1885)	+	+	+							+	+			+	
<i>Aporrectodea rosea</i> (Savigny 1826)	+	+	+	+		+		+		+	+				
<i>Aporrectodea trapezoides</i> (Dugès 1828)	+	+	+	+		+	+	+	+	+	+			+	
<i>Aporrectodea tuberculata</i> (Eisen 1874)	+		+	+		+	+	+		+	+			+	
<i>Bimastos parvus</i> (Eisen 1874)	+		+	+		+	+	+		+	+			+	+
<i>Bimastos tumidus</i> (Eisen 1874)										+	+				
<i>Dendrobaena attensi</i> (Michaelsen 1902)	?	?								+					
<i>Dendrobaena hortensis</i> (Michaelsen 1890)	B+		*							+				+	
<i>Dendrobaena octaedra</i> (Savigny 1826)				+				+		+	+			+	
<i>Dendrobaena pygmaea</i> (Savigny 1826)				*						+					
<i>Dendrobaena veneta veneta</i> (Rosa 1886)	B+		*							+					
<i>Dendrodrilus rubidus rubidus</i> (Savigny 1826)	+	*	+	+		+		+		+	+	+	+	+	
<i>Dendrodrilus rubidus subrubicundus</i> (Eisen 1874)	+									+					
<i>Dendrodrilus rubidus tenuis</i> (Eisen 1874)	+	+		+		+		+		+					
<i>Eisenia fetida andrei</i> Bouché 1972	+		+	+		+	*			+	+	+	+	+	
<i>Eisenia fetida fetida</i> (Savigny 1826)	+	*	+	+		+		+		+	+	+	+	+	
<i>Eisenia japonica</i> (Michaelsen 1892)				+		+		+							
<i>Eisenia nordenskioldi</i> (Eisen 1879) ssp. Emend.						+		+				+			

<i>Eiseniella tetraedra</i> (Savigny 1826)	+	+	+	+	*	+	+	+	+	+
<i>Eophila moebii</i> (Michaelsen 1895)									+	
<i>Eophila molleri</i> (Rosa 1889: 3)								+	+	
<i>Lumbricus castaneus</i> (Savigny 1826)	*		*	+				+	+	+
<i>Lumbricus festivus</i> (Savigny 1826)	+							+		
<i>Lumbricus friendi</i> Cognetti 1904	+							+		
<i>Lumbricus rubellus</i> Hoffmeister 1845	+		+	+	+	+	+	+	+	+
<i>Lumbricus terrestris</i> Linnaeus 1758			*	+	+	+	+	+	+	+
<i>Murchieona minuscula</i> (Rosa 1906)								+		
<i>Murchieona muldali</i> (Omodeo 1956)								+		
<i>Octolasion cyaneum</i> (Savigny 1826)	+		+	+				+	+	+
<i>Octolasion tyrtaeum lacteum</i> (Örley 1881)	*?			+				+	+	+
<i>Octolasion tyrtaeum tyrtaeum</i> (Savigny 1826)	+							+	+	+
<i>Satchellius mammalis</i> (Savigny 1826)								+		
Ocnodrilidae (Tropical America and Africa)										
<i>Gordiodrilus elegans</i> Beddard 1892	*							+	+	+
<i>Nematogenia panamaensis</i> (Eisen 1900)								+	+	
<i>Ocnodrilus occidentalis</i> Eisen 1878	*		*		+			+	+	+
<i>Eukerria kuekenthali</i> (Michaelsen 1908)	+							+	+	+
<i>Eukerria saltensis</i> (Beddard 1895)	+		*?		*			+	+	+
<i>Malabarica levis</i> (Chen 1938)								+		+
<i>Thaonia exilis</i> Gates 1945								+	?	+

(Continued)

Table 14.1 (Continued)

Families (origins) and Species from Regions	Mainland Australia (excluding Tasmania)	Tasmania	N.Z.	Japan (excluding Ryukus)	Ryukyu Islands	Korea (including Cheju Island)	Taiwan	China (including Hainan)	SE Asia	USA and Canada	Mexico	Hawaii	P.I. Lanka	India and Sri Lanka	Myanmar (Burma)
<i>Thaonia gracilis</i> Gates 1942									+						+
Acanthodrilidae (Pangean?)															
<i>Microscolex dubius</i> (Fletcher 1886)	+	*	+							+	+			+	
<i>Microscolex kerguelarum</i> (Grube 1877)	+(H)														
<i>Microscolex macquariensis</i> (Beddard 1896)		+(M)													
<i>Microscolex phosphoreus</i> (Dugès 1837)	+	*	+	+						+	+			+	
<i>Rhododrilus kermadecensis</i> Benham 1905	B+?	*											+		
<i>Rhododrilus queenslandicus</i> Michaelsen 1916	+														
<i>Rhododrilus</i> sp. north Queensland	+														
Octochaetidae (Circumtropical, plus Indo-Australasia)															
<i>Dichogaster affinis</i> (Michaelsen 1890)	*							+(H)	+	+	+			+	+
<i>Dichogaster annae</i> (Horst 1893)	*								+		+			+	+
<i>Dichogaster bolau</i> (Michaelsen 1891)	++(Cl)				+		+	+(H)	+	+	+			+	+
<i>Dichogaster corticis</i> (Michaelsen 1899)									+						
<i>Dichogaster modiglianii</i> (Rosa 1896)	+(Cl)								+	+	+			+	+
<i>Dichogaster reincke</i> Michaelsen 1898													+		
<i>Dichogaster saliens</i> (Beddard 1893)	*+(Cl)				+				+	+	+			+	+
<i>Dichogaster</i> sp. nov? in NT	*														
<i>Lenmogaster pusillus</i> (Stephenson 1930)									+						
<i>Octochaetona beatrix</i> (Beddard 1902)	*								+						+

Table 14.1 (Continued)

Table 14.1 (Continued)

Families (origins) and Species from Regions	Mainland Australia (excluding Tasmania)	Tasmania	N.Z.	Japan (excluding Ryukus)	Ryukyu Islands	Korea (including Cheju Island)	Taiwan	China (including Hainan)	SE Asia	USA and Canada	Mexico	Hawaii	P.I.	India and Sri Lanka	Myanmar (Burma)
<i>Pithecha bicincta</i> (Perrier 1875)	++ ^(CI)			+	+		+	+	+	+	+	+	+	+	+
<i>Polypheretima annulata</i> (Horst 1883)									+						
<i>Polypheretima brevis</i> (Rosa 1898)	+ ^(CI)												+		
<i>Polypheretima elongata</i> (Perrier 1872)	+				+		+		+	+	+	+	+	+	+
<i>Polypheretima taprobanae</i> (Beddard 1892)	+									+	+	+	+	+	+
<i>Polypheretima voeltzkowi</i> (Michaelsen 1907)											+	+	+	+	
Eudrilidae (West African)															
<i>Eudrilus eugeniae</i> (Kinberg 1867)	*									+	+			+	
Total nonendemic exotic spp. (E)	66	27	27	34	18	23	30	47	58+	60	46	33	30	50	50
Endemic natives in region (N)	449	203	172	40	10	70	41	196	?	122	57	0	20	455	135
Approximate total spp. (E + N)	515	230	199	74	28	93	71	243	?	182	103	33	50	505	185
Exotics [E/(E + N)] approximate (%)	12.8	11.7	13.6	46.0	64.3	24.7	42.3	20.0	?	33.0	44.6	100	60.0	9.9	27.0
Region	Mainland Australia	Tasmania	N.Z.	Japan	Ryukyu	Korea	Taiwan	China	SE Asia	USA and Canada	Mexico	Hawaii	P.I.	India	Myanmar
Approximates															
Lumbricidae as % total exotic	35	60	67	38	0	57	20	28	6	53	46	33	10	34	4
Megascotlecidae as % total exotic	35	18	22	47	72	39	73	51	63	28	26	51	66	34	56

Abbreviations: + = present as a nonendemic species; * = first records from author's (R.J. Blakemore) studies; ? = indicates some ambiguity of taxonomy, endemism (e.g. possibility that the taxon is native to a region) or veracity of report; B = J.C. Buckerfield, pers. comm.; ^(ab) = Bonin Island; ^(ci) = Christmas Island; ^(th) = Heard and McDonald Islands; ^(mt) = Macquarie Island; ^(v) = Torres Straits Islands; N.Z. = New Zealand; P.I. = Pacific Isles (Fiji, Samoa, Tonga, Niue I., Kermadec, Vanuatu, Cook Isles, Tahiti, Marianas, Marshalls, Carolines, Marquesas, New Caledonia with Loyalty Islands)—reports from Easton (1984) and Lee (1981).

terms “alien,” “exotic” and “invasive” are often used interchangeably, and “peregrine” meaning “wanderer” or “wandering” as first used by Michaelsen (1903) to describe earthworms that are dispersed over a wide range and in geographically remote localities, the definition of “cosmopolitan” is less precise, meaning either widely distributed in many parts of the world or merely present in more than one country, but with the ecological implication of passive or unintentional transportation.

Of some 9,000+ named terrestrial and aquatic oligochaetes (as calculated below), about 6,000 are earthworms with only 120 species (plus synonyms) widely distributed and commonly encountered throughout the world—comprising 47 Megascolecidae (mainly pheretimoids), 33 holarctic Lumbricidae and 40 or so species from some of the 18 other families (Blakemore 2006a). Lee (1985) proposed that only about six lumbricids and the same number of tropical species have life histories adequately revealed, and Reynolds (1998) claimed that detailed ecological studies have been made on fewer than 20 earthworm species. However, Blakemore (1994, 1997a) surveyed and studied 30 earthworm taxa—including several species new to science—in a series of laboratory, glasshouse and field experiments. Since then, Barois et al. (1999) provided basic ecological data for nearly 60 tropical species, and Omodeo et al. (2004) reported ecological and biogeographical traits of some of their 38 Maghreb megadriles.

14.2 NUMBER OF EARTHWORM SPECIES

In the century following Michaelsen’s (1900) *Das Tierreich: Vermes* review of all 1,200 oligochaete species then known, taxonomic efforts have overwhelmed and polarized researchers either toward the aquatic and usually smaller microdriles or toward the generally larger terrestrial megadriles (the “true” earthworms). Subsequent totals were based on estimates by Lee (1985, 1987) of ~3,000 megadriles (with just 100 peregrine species), and on a statement by Reynolds (1994) of nearly 8,000 described Oligochaeta, though citing only “Reynolds and Cook (1993),” who tallied just 7,254 species with 3,627 (~50%) terrestrial megadriles (and presumably 3,627 microdriles).

The current, incomplete ZooBank total for Oligochaeta is 7,585 taxa including both megadrile and microdrile species, while other estimates exceed 8,000. A reasonable total, however, is closer to ca. 5,900 named terrestrial megadriles, and, including aquatic microdrile estimates, we reach a conservative total of 9,500–10,200 nominal Oligochaeta taxa with an unknown number of synonyms. Yet probably less than 25–30% of earthworms from around the world have been described. For instance, Tasmanian studies have increased the species total of this allegedly well-studied island fourfold, from 55 to 230 taxa (Blakemore 2000c), and recently added names have nearly doubled the faunas of Australia, Japan, Taiwan and some other Asian countries (see Blakemore 2002, 2003, 2005, 2006a, b), while South American, Middle Eastern and African faunal lists are far from complete.

In comparison, the marine Polychaeta has ~13,000 named taxa (and ZooBank lists just 10,755 spp./genera), although only ~8,000 of these are considered reasonable species. The apparently high diversity among polychaetes is due partly to a greater number (perhaps 10-fold) of full-time researchers for this group. Considering that >99% of the world’s food (and fiber) supply is produced on land, whereas only 0.6% comes from oceans and other aquatic ecosystems (FAO 1991), underfunding of soil ecotaxonomic research in favor of marine taxonomic ventures is arguably an unbalanced economic decision.

14.3 CHARACTERISTICS AND ORIGINS OF COSMOPOLITAN EARTHWORMS

Cosmopolitan earthworms have a propensity for transportation and tend to have some or all of the following characteristics: small size, parthenogenic or asexual reproduction such that a single specimen may start a colony (Gates 1972; Sims and Gerard 1999), high fecundity, resistant cocoons, wide environmental or feeding tolerances (eurytopicity), and rapid dispersal rates (Lee 1985, 1987; Blakemore 2002); they may also lack specialized predators in their new lands. Moreover, Gates (1968, 1972) commented that parthenogenesis, often accompanied by polyploidy, permits more rapid accumulation of mutations than if reproduction had remained amphimictic, and that parthenogenetic morphs seem to withstand higher parasitic burdens, possibly because less bodily resources are allocated to reproduction. The ability of an individual or species to survive in a location after its introduction is thereafter influenced by local climate, soil ecology and soil management practices.

Family origins of cosmopolitan earthworms often correspond to the eight independent centers of the world's major cultivated plants (Vavilov 1951; see Table 14.1). Species associations indicate that certain earthworms may have accompanied some plants via agriculture and world trade, but transportation of earthworms into nonindigenous regions, as with crops, is not necessarily via the most direct route. Evidence for such spread is the faunal lists for the Levant and Maghreb (Csuzdi and Pavlicek 1999, 2005; Omodeo et al. 2004; Pavlicek et al. 2004) having several earthworm names familiar to workers in other regions of the world where cultivated plants originally from the Middle East and Mediterranean now grow, and vice versa. The likelihood that routes may be indirect and that the most probable mechanism of introduction is human-mediated transportation are supported by continued interceptions by national quarantine services (e.g. those reported by Gates 1972 and Lee 1987).

Native species may also be translocated within a bioregion by mechanisms similar to those pertaining to exotics: some examples are reported within the Australian genus *Anisochaeta* spp. in Tasmania (Blakemore 1999, 2000a, c; see Table 14.1) and probably for *Bimastos* spp. in North America (Hendrix 1995). Establishing translocation for a native relies on evidence including exact morphological and/or molecular match, a noticeably disjunct distribution and prevalence in the new domain mainly in disturbed habitats such as gardens or fields or other probable mechanisms of transport such as fishing bait.

Apart from determining whether native taxa are new or translocated, one of the challenges in ecological taxonomy is to reliably distinguish exotics from natives and to assess the diversity and distribution of both (e.g. Blakemore 1999; Omodeo et al. 2004; Pavlicek et al. 2004). Faunal comparisons help us appreciate mechanisms of ecosystem functioning and are crucial for understanding regional biodiversity and monitoring the spread of human-mediated species transportations and extinctions.

14.4 OVERVIEW OF RESULTS

This chapter summarizes field and literature surveys, compiled into regional faunal lists allowing for most current taxonomic treatments, based on the author's independent studies as well as on various other sources (as acknowledged in the text). Previous regional species totals from the literature are found, for example, in Michaelsen (1900, 1903), Gates (1972), Sims (1980), Sims and Gerard (1985, 1999), Lee (1985, 1987), Julka (1988), Hendrix

(1995), Fragoso et al. (1995, 1999, 2004), Blakemore (1999, 2000c), Tsai et al. (2000), Fragoso (2001) and Blakemore (2003, 2004a–f, 2005, 2006a, b). Relative proportions of natives to exotics from selected regions are compared in Fig. 14.1, with data extracted from distributional species lists found outside their endemic domains, as presented in Table 14.1. Not all cosmopolitans are listed and, naturally, species are not considered exotic in regions where they are thought to be endemic; nevertheless, they may be subject to translocation there. Moreover, several cosmopolitan species are now so ubiquitous that their origins are obscure or questionable. Blakemore (2002, 2006a) provides detailed descriptions with figures, synonymies, distributions and ecological information for all ~120 known cosmopolitan earthworms, and these will be the main subjects of further discussion. Regions of the globe for which total species checklists are currently compiled and available (e.g. Blakemore 2006b) are shown in Fig. 14.2.

14.5 DISCUSSION

Meaningful biodiversity comparisons require representative estimations from reliable survey (e.g. considering numbers and size of samples, soil depth, various habitats and seasonal differences) and correct identification of community components (specific and ecological categorization). Difficulties include the amount of work required for adequate sampling and hand sorting of soils, and the lack of complete and consistent species guides (Table 14.2).

One day's field sampling often results in at least a fortnight's laboratory/library work for identification, which is why museum shelves around the world are stacked with voucher specimens awaiting identification by specialists. Solutions include implementing standard quantitative and qualitative sampling methods, such as those provided by ISO 23611-1 (2006), and support for the compilation of detailed, comprehensive taxonomic guides that include all known species (as well as those potentially occurring) within a region, rather than using limited "species identifiers" that tend to force choices into one or two species and often lead to false results (Blakemore 1999, 2002, 2006a).

Some species tend to be small in size and, apart from being easily overlooked, are often difficult to identify or are dismissed as immatures. Examples of small worms include several *Drawida* spp., *Eukerria saltensis*, *Gordiodrilus elegans*, *Ocnodrilus occidentalis*, *Dichogaster* spp., *Dendrobaena* spp., *Helodrilus oculatus*, *Murchieona minuscula* and some *Amyntas* spp. such as *Amyntas minimus* (see Table 14.1). When such omissions and identification errors are corrected, biodiversity results can be considerably higher. Lavelle (1978), for example, recorded up to 13 species from savannas and gallery forest sites at Lamto, Ivory Coast; Abbott (1985a, b) identified exotics and 62 native "morpho-species" representing an unknown number of taxa from jarrah (*Eucalyptus marginata*) forests in Western Australia; a regional study by Bano and Kale (1991) in southern Karnataka, India recorded 44 species (eight exotic); Omodeo et al. (2004) reported 38 megadrile species in 2,110 specimens from 177 sites of the Maghreb, North Africa; and Omodeo and Rota (1989) described 51 species (14 new) from ca. 2,000 specimens from 50 localities in Turkey collected between 1987 and 1988. In the Levant, 34 species are currently known with about a dozen (40%) cosmopolitan or introduced (Pavlicek et al. 2004). Recent surveys in Taiwan by Chen et al. (2003) found 42 species, and a transect by Tsai et al. (2004) collected 2,163 specimens from 43 samples at 27 localities and recorded 34 earthworm species including 14–15 exotics. A weeklong survey on shorelines at Lake Pedder in western Tasmania revealed 21 species with 16 natives, 5 exotics plus 3 aquatic

Regions of the globe with earthworm checklists

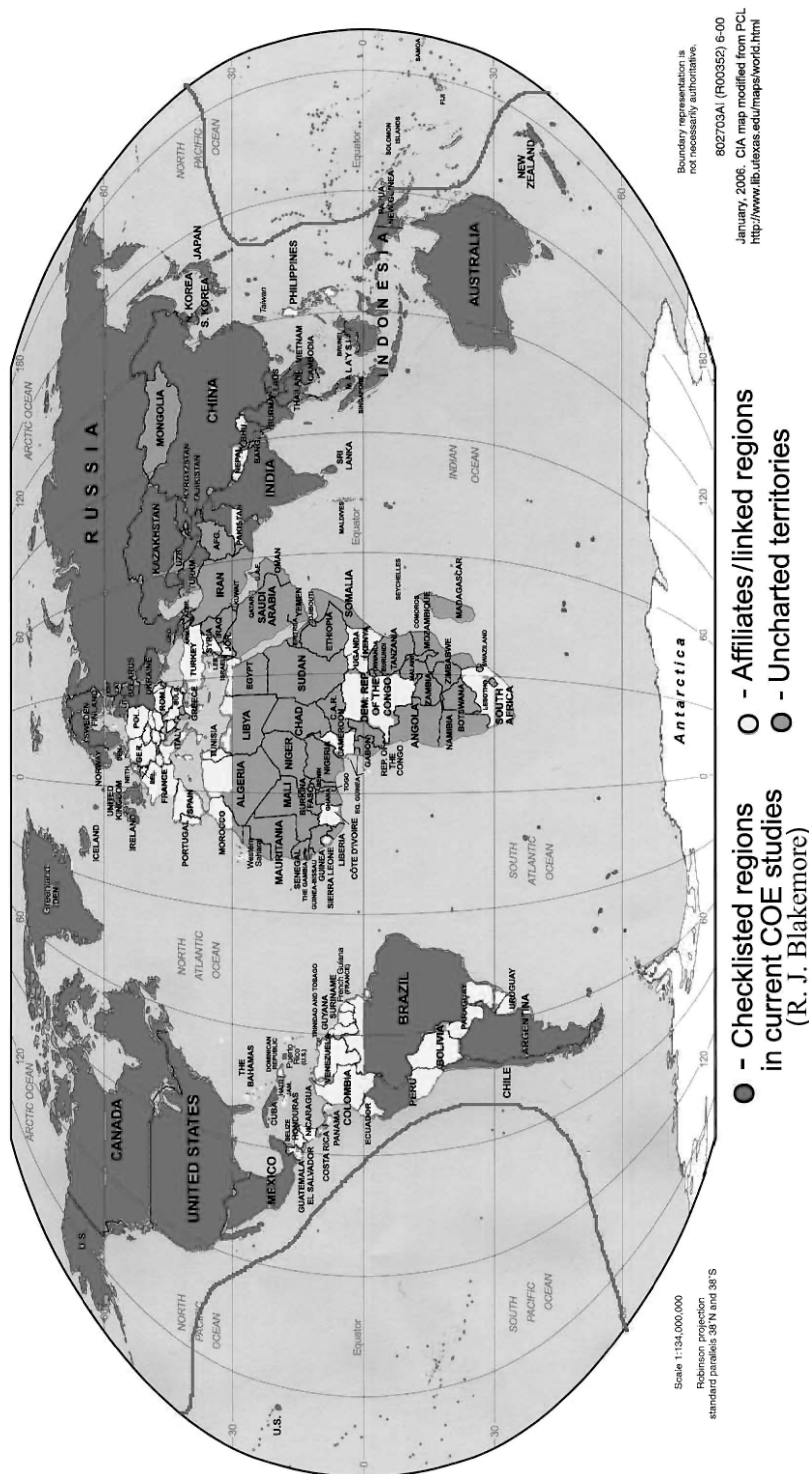


Figure 14.1 Regions with current checklists of earthworm species. (See color insert.)

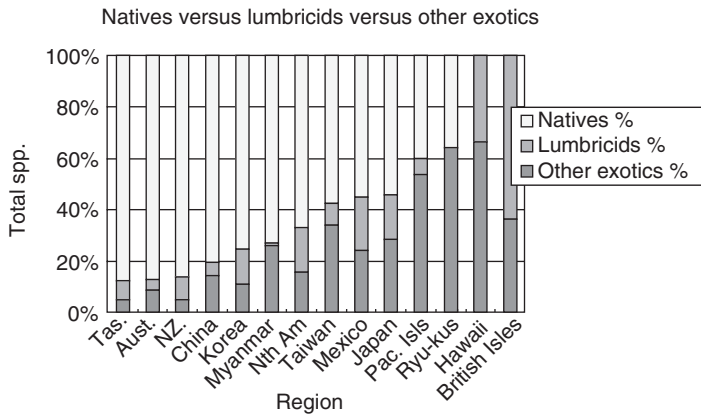


Figure 14.2 Lumbricidae as a proportion of total species from selected regions (only British Isles have >40%). Abbreviations: Tas = Tasmania; Aust = Mainland Australia; N.Z. = New Zealand; Nth Am = North America (Rio Grande to Arctic); Pac Isls = Pacific Isles (not Hawaii); China = China + Hainan. (See color insert.)

Table 14.2 Contingency table of sampling reliability

Case	Ecological Sampling	Taxonomic Treatment	Results
1	+	+	Representative data
2	+	–	Under / overestimate
3	–	+	Under / overestimate
4	–	–	Unrepresentative data

Abbreviations: + = good; – = poor.

microdriles (Blakemore 2000a), while a dozen species were found in a brief survey around Lake Biwa, Japan (Blakemore 2007b). Other notable earthworm biodiversity surveys include 24 species (with 16 exotics) from ca. 100 ha of a mixed farm property systematically sampled monthly for 2 years at Samford, southeast Queensland where a Brisbane regional total exceeded 40 species (Blakemore 1994, 1997a), and 14 species (with 10 exotics) collected one weekend on a 45-ha farm in the Southern Highlands of New South Wales (Blakemore 2001a, b). These high figures exemplify the need for more extensive and, at the same time, more intensive combinations of both ecological survey and taxonomic analysis. Therefore, the statement by Lee (1985) that earthworm species diversity is fairly consistent in different regions and habitats, ranging from 1 to 11 species and most commonly just two to five, should perhaps be revised upwards.

14.6 REGIONAL SPECIES TOTALS AND PROPORTIONS OF EXOTICS

Checklists show that the Oriental pheretimoids (family Megascolecidae) now comprise some 980 valid names from >1,200 nominal taxa, and the holarctic lumbricids (family Lumbricidae) total 670 valid names from ~1,150 nominal taxa (Blakemore 2006b). These two groups contribute two-thirds of the ~120 total cosmopolitan species, while the remaining third has diverse origins in various other families (see Table 14.1). Earlier accounts of exotics have tended to overemphasize the importance of the lumbricids, perpetuating

misinformation that they are the major earthworm group, partly because they are common in temperate regions, but mainly because lumbricids are more familiar to workers in Europe and in North America, whereas identification guides for other groups are generally lacking (cf. Gates 1972). Based on current data, interchanging the terms “earthworms” and “Lumbricidae” appears unwarranted as lumbricids are dominant only in temperate regions of northern Europe and the Middle East, and in other regions are often a minor component of the total fauna (see Table 14.1). For instance, when Fragoso et al. (1999) compiled survey data from the humid tropics worldwide, they found 51 common exotics, but just 17 (33%) of these were Lumbricidae. The relative proportions of Lumbricidae including *Eisenia japonica* (Michaelsen 1891), which is supposedly endemic to Korea, Japan and the Siberian Kurils, and the Megascolecidae—mainly Asiatic pheretimoids—are compared to other exotics as summarized in Table 14.1 (cf. Fig. 14.2 derived from this data).

Earthworm diversity in Australia including Tasmania now totals 715 (sub)species, of which 65 are exotics (~9% of total with just ~3% lumbricids); of these, ca. 20 are new records from the author’s modest studies including the first Australian report of *Lumbricus terrestris* Linnaeus 1758 from Tasmania (Blakemore 1997b). Continued ecotaxonomic surveys are likely to double the number of Australian natives, and further exotics are expected. Moreover, if all *Begemius* Easton 1984 (Megascolecidae from Papua New Guinea) and *Rhododrilus* Beddard 1889 (Acanthodrilidae from New Zealand) species are included as exotics/neoendemics, then the total of ~80 exotics is considerably higher than a previous calculation of just 27 mainly Lumbricidae species (see Blakemore 1999). Unlike mainland Australia and New Zealand, no native Acanthodrilidae or Octochaetidae are known from Tasmania.

India and adjacent countries including Sri Lanka have 505 described earthworm taxa, only 50 (<10%) of which are exotics and fewer than 18 (3%) Lumbricidae (the native species tend to be within the families Moniligastridae, Octochaetidae and Megascolecidae). In comparison, the tally for China (including Hainan but excluding Taiwan), which is dominated by Megascolecidae (~200 spp.) followed by Moniligastridae (~20 spp.), is now 244 species with 47 (20%) exotics and just 13 (5%) Lumbricidae. Both India and China have long and diverse histories of cultural exchange and are likely sources of several cosmopolitan earthworms. Neither country has confirmation of any native Lumbricidae, Acanthodrilidae nor Glossoscolecidae.

Japan, including the Ryukyus (Okinawan Islands), has 80 earthworm species (50% exotic), and while no Lumbricidae are yet known from tropical Okinawa, a new record from there (Blakemore et al. 2007) is for *P. corethrurus*. The Korean peninsula including volcanic Cheju (Quelpart Island) has 93 species with 23 exotics (24%), and about half of these are Lumbricidae; however, unlike most other oriental countries where both native and exotic faunas are more often dominated by Megascolecidae and Moniligastridae, the cooler Korean climate appears to allow a relatively greater abundance of hol-arctic Lumbricidae including putative natives *E. japonica* (Michaelsen 1892) and *Eisenia koreana* (Zicsi 1972). The island of Taiwan has 71 known earthworm species, 30 of which are considered exotics (42%), but at least an additional 30 undescribed natives are known (Chen et al. 2003; Blakemore et al. 2006), and just six (20%) of the exotics are Lumbricidae. Only three Lumbricidae are known from Myanmar (formerly called Burma and part of British India), which has 185 species with 50 (<30%) exotics (Gates 1972; Blakemore 2005). Totals for all other Southeast Asian countries are unknown, although 41 exotic species are reported and just three of these are Lumbricidae (see Table 14.1).

Several Asiatic species are now distributed worldwide, for example, *Drawida barwelli* (Beddard 1886), *Amyntas gracilis* (Kinberg 1867) and the *Amyntas corticis* (Kinberg 1867) species complex that Gates (1972) thought might have been transported more widely than the better-known lumbricids. Erstwhile reports from North America of components of the *Metaphire hilgendorfi* (Michaelsen 1892)/*Amyntas tokioensis* Beddard 1892 species complex (e.g. Gates 1958; Hendrix 1995; Hendrix and Bohlen 2002) are thought to have originated from Japan (or possibly China) (see note on Perry's "Black Ships" below).

Continental North America, north of the Rio Grande, has relatively poor faunal diversity due to its division by epi-eric seaways in the Cretaceous, and subsequently by extensive glaciation as recently as the Pleistocene (~18,000 years ago). Two endemic lumbricid genera are *Bimastos* and *Eisenoides*; thus, the earliest likely period for commencement of the wider distribution of cosmopolitan *Bimastos parvus* (Eisen 1874) outside America follows the European colonization 500–1,000 years ago. A total of 182 species in 12 families, with about 60 (~33%) exotics was compiled by Blakemore (2005), compared to Reynolds and Wetzel (2004) and Wetzel (2003, 2007), who report 161 megadriles in 10 families from the same region, including 45 exotics for which several names are invalid or have long been superceded (e.g. *Aporrectodea turgida*, *Eisenia fetida*, *Amyntas hawayanus*, *Amyntas diffringens*; cf. Sims and Gerard 1985, 1999; Blakemore 1999, 2002).

Mexico has 104 described species, with 46 (~45%) thought to be post-Columbian introductions; of these exotics, less than half are Lumbricidae. Other South American totals include 240–260 oligochaetes in Brazil and 320–350 neotropical species (Fragoso et al. 2004), while Latin America as a whole now has 830 described earthworm species with ~70 (8.4%) exotics and just 35 Lumbricidae (i.e. half of the exotics or just 4.2% of total species) as catalogued by Dr. G. Brown (see Brown and Fragoso 2007).

Volcanic Hawaii harbors 50 nominal earthworm taxa but with just 33 valid names (Blakemore 2006b), and all are introduced exotics, whereas all other Pacific Isles have about 50 species with 30 (~60%) considered exotics, of which just three are Lumbricidae (Blakemore 2005, 2006b; see Table 14.1).

14.7 EARTHWORMS, ARCHAEOLOGY AND HUMAN HISTORY

Regarding the "humble earthworm," Darwin (1881) stated, "It may be doubted whether there are many other animals which have played so important a part in the history of the world, as have these lowly organized creatures ..." and "The vegetable mould [humus] which covers, as with a mantle, the surface of the land, has all passed many times through their bodies."

Although Darwin mainly commented on their intimate ecological relationship with soils and plant growth, his contributions to earthworm study also extended into the realms of anthropology and archaeology; e.g. an experiment on surface casting and the burial of objects was judged as being essential to archaeological excavation (Darwin 1840), and was corroborated by Keith (1942) and Jewell (1958)—see also Hart and Terrell (2002). Remains of invertebrates or other animals often provide archaeological evidence (Steadman 1995; Morrison 1996a, b; Grayson 2001), but unlike small or winged organisms that are carried by the wind, earthworms are less actively mobile, and most (native) species have highly restricted distributions—suitable criteria for indicator taxa to investigate human transportations. Current earthworm populations may be indicative of past human

movements, but because their soft bodies rapidly decompose, only the preservation of their chitinous setae (McCobb et al. 2004), fossilized embryos and cocoons (Schwert 1979; Pearce et al. 1990, 1992; Manum and Bose 1991), and calciferous glands (Gates 1972) provide evidence for environmental archaeology.

Recent DNA analyses show that early humans traveled widely from an African origin. Only in relatively recent times have humans had the technical ability to transport substantial amounts of rocks or soils with resident earthworms. Preagricultural people carried few tangibles, and only after the advent of the agricultural era did muscle power from domesticated draft animals (or humans) cultivate and move large quantities of soil. These processes intensified during the mechanization of the Industrial Age and have accelerated under the current globalization of world trade associated with the transition to an information-based economy (Toffler 1980), now tempered with implementations of quarantine barriers, wildlife legislation and import restrictions as applied to plant, animals, soils and soil products.

Agriculture or pastoralism developed independently in several regions including the Middle East, Africa, India, Asia, Sahul, Mesoamerica and the Andes about 10–12,000 years ago (Vavilov 1951). Transportation of earthworms out of the Middle East may have followed the spread of agriculture throughout Europe in the Neolithic era, yet voyages and settlements by Europeans responsible for the global transportation of earthworms into the New World, South Africa and Australasia are thought to have commenced only in the last 1,000 years (Gates 1972; Enckell and Rundgren 1988). *Dendrobaena octaedra* (Savigny 1826) was found in Greenland “in districts inhabited by the Norse ten centuries ago” (Gates 1972), and it also inhabits Hokkaido (Stöp-Bowitz 1969), although just how much of this species’ present range is self-acquired is unclear as its dispersal is thought to be restricted only by its freeze tolerance (Berman et al. 2001). Possible examples of prior species redistributions within Western Europe are the small *Satchellius mammalis* (Savigny 1826) found in Germany, Spain, the British Isles and Ireland, an area coincident to the region settled by the Celts, as noted by its synonym *Allolobophora celtica* Rosa 1886, and a similar distribution pertains to *Dendrobaena attemsi* (Michaelsen 1902) (see Rota and Erséus 1997; Fig. 14.1)—both taxa recently recorded as introduced to the USA. Finding the similarly small *H. oculatus* Hoffmeister 1845, with a natural distribution in western and eastern Europe, in a Roman ditch in Verulamium (St. Albans, UK) led to speculation that the species may have been introduced to Britain during the Roman occupation, if not earlier (Dobson and Satchell 1956).

That some exotic Lumbricidae (except perhaps *Bimastos*) originated in the “fertile crescent” of the Middle East and were subsequently transported along with agriculture is supported by presence of ~10 cosmopolitan species in the Levant (Paylicek et al. 2004; Paylicek 2006) in common with those found in the British Isles (Sims and Gerard 1999). Reflecting its colonial history, almost all the 30+ Lumbricidae now recorded in Australasia/North America correspond to those known from the British Isles that themselves probably originated from Continental Europe. Australia had remained remote from most world trade until the mid-1800s, and only in the last 500 post-Columbian years can regular exchange account for the distributions of certain European species in the Americas. Fletcher (1886) quotes letters in “*Nature* (1884)” that earthworms did not originally exist in the prairies of the Canadian Northwest nor in parts of the USA (i.e. Kansas, Idaho, and the Indian and Washington Territories).

However, in the mid-15th century (nearly a century before Columbus landed in the Americas), sailors such as Admiral Zheng He established trade routes and bases from China through Southeast Asia as far as India, the Middle East and East Africa. Prior to this,

Indonesian, Indian, Arab, Scandinavian, Japanese and Chinese seafarers, missionaries (e.g. Ibn Battuta), explorers, invaders, refugees, pirates and overland traders using routes such as the Silk Road(s) have exchanged commodities including animals and plants. Ancient trade routes, partially over land and partially by sea, linked Mediterranean Attica and Rome to cultures of the Indus Valley and the east coast of India as long as 2,400 years ago. Also, for at least the last three millennia, Polynesian and Melanesian people (carrying with them food plants such as taro) migrated in the Pacific wherein “coral island taxa,” those earthworms dispersed by pre-Columbian voyagers, were distinguished from “tropical tramps,” species probably introduced after Europeans entered this region (Lee 1981, 1985, 1987).

Thus, the origins and current distributions of earthworms can likely help track early human migration routes; e.g. dispersal of some cosmopolitan species predate the movement of European explorers and reflect earlier, largely undocumented wanderings and commerce within the Pacific and Indian Oceans. Gates (1972), for instance, found the disjunct distribution of the aquatic Almidæ genus *Glyphidrilus* Horst 1889 in Tanzania and in Southeast Asia difficult to interpret by overland transport from an African origin. However, its distribution may be attributed to sea carriage from Asia, possibly via India or Sri Lanka, considering that Madagascar, and possibly the east coast of Africa (where *Glyphidrilus stuhlmanni* Michaelsen 1897 occurs), was colonized from about 1,500 to 2,000 years ago by seafaring people originating from Borneo (where *G. kuekenthali* Michaelsen 1896 occurs), and that these or successive people (see Hules et al. 2005) conceivably transported soil with their plant rootstocks or specimens in their water supplies. Ljungstöm (1972) had considered that six peregrine species of Oriental *Pheretima* found along the eastern coast of South Africa were associated with such early human trade. Conversely, Stephenson (1931) speculated that the often small-sized members of the genus *Dichogaster* “have probably been carried eastwards from Africa in successive stages, perhaps accidentally by early man in his wanderings, in his belongings, or later in merchandise of one sort or another.”

For the Asia Pacific region, Sims and Easton (1972) proposed that “man has always been moving among the islands: from prehistoric times onwards successive waves of colonists have spread out from the mainland of Asia while at present some small atolls are occupied only temporarily. In these circumstances, earthworms and their cocoons may unwittingly have been transported in the soil packed around the roots of the crops which these travelers have in all probability taken with them.” Dispersal of *Drawida japonica* (Michaelsen 1892) is thought to be from China to Japan, possibly via Taiwan (Blakemore 2003), although Gates (1972) speculated that this species came originally from the Indian Himalayas, and Yunnan and Szechuan in China. Introduction of other species into Japan, e.g. the lumbricid *E. japonica*, may be linked with earlier occupants such as the Ainu people from Siberia. On the other hand, some *Amyntas* and *Metaphire* pheretimoids are either native, neoendemics or are introductions from earlier times, possibly corresponding to the Jomon period when land bridges connected Japan to the Asian mainland. Global transportation of several of these Japanese species probably commenced with reopening of ports after two centuries of isolation following Commodore Perry’s “Black Ships” arrival near Yokohama on July 8, 1853.

Other pheretimoids, such as *Pheretima*, *Begemius* and *Polypheretima*, are indigenous to New Guinea and parts of the Indonesian archipelago—areas of ancient agricultural development—and all three genera have restricted and patchy distributions on adjacent islands and in northern coastal Australia characteristic of imported species (Blakemore 1994, 1999, 2003). Because *Polypheretima brevis* (Rosa 1898) on Christmas Island (Australian territory) and Tonga and *Po. pentacystis* (Rosa 1891) in the Seychelles and

Madagascar both occur outside the normal Oriental “*Pheretima* domain,” Easton (1979, 1984) proposed that they were introduced by (early?) human agency and found no evidence to explain transoceanic distributions of some other Pacific *Pheretima* species by natural means. Thus *Polypheretima voeltzkowi* (Michaelsen 1907) is thought to have been introduced to the Comoros, possibly from New Guinea since Lee (1981) called it a “Melanesian species,” and was also introduced to Vanuatu. Remote UNESCO World Heritage Easter Island and Henderson Island in the South Pacific, both populated by Polynesian people, have a few pheretimoids [e.g. *Amyntas hendersonianus* (Cognetti 1914)] that have subspecies in New Guinea (Blakemore 2005), as well as *E. saltensis* that originates from South America.

Earthworms may yet help trace undocumented human movements such as those by Macassan seafarers from southwest Sulawesi (formerly Celebes) who are known since the 1300s to have traded a Chinese and Indonesian delicacy, the trepang (dried Holothurian sea slugs) obtained from coastal Arnhem Land in Australia (MacKnight 1976). This could partially account for restriction in Australia of Indonesian *Polypheretima elongata* to a few localities in northern coastal Queensland (Easton 1976; 1982; Blakemore 1994). Distribution of earthworms on the Pacific islands may help explain the enigmatic Lapita culture complex that perhaps originated in the Bismarck Archipelago. The extent of contact and trade that occurred in ancient times is not well-known, but certainly a long period of human occupation in Australia and the Sahul has dates now thought to extend 60,000–120,000 years ago (e.g. Singh et al. 1981; Wright 1986).

In New Zealand, possibly the last habitable place on the planet where permanent human settlement commenced only around 2,000 years ago (Grayson 2001), at least eight kinds of earthworms—including *Rhododrilus edulis* Benham 1904—were formerly used as prized dishes in Maori feasts (Stephenson 1930). Two *Rhododrilus* are known from Australia’s coast: *Rhododrilus queenslandicus* Michaelsen 1916 from northern Cape York Peninsula and *Rhododrilus kermadecensis* Benham 1905 from southern Tasmanian tidal mudflats, also reported from Kangaroo Island in South Australia (Blakemore 1999, 2000c). Probably not endemic to Australia, such species may have been introduced and have become naturalized following introduction, or possibly they are relict fauna of ancestral stock shared with other regions and are now isolated (Blakemore 1994). Although prevailing ocean currents are in the opposite direction (from East to West), such worms (along with plants) were possibly carried by boat from New Zealand during unrecorded ephemeral visits by Maori explorers.

Recently, Fragoso et al. (1999) and Gonzalez et al. (2006) attempted to relate Caribbean distributions of exotic earthworms with the African slave trade, noting that the occurrence of some species may be explained by human migration prior to European colonization, possibly due to “island hopping” by indigenous people from South America up to 2,200 years ago.

The process of species transportation continues to date, for example, when neighbors exchange potted plants containing earthworms, or when European cypress (*Cupressus sempervirens*) planted on a dam in Argentina are the likely source of lumbricid *Octodrilus* spp. (Mischis and Brigada 1988; Mischis 2004). Similar accidental imports are also evidenced by the large number of new species described from botanic gardens, although control measures have been stricter since the 1940s such that Gates (1972) cited the interception of 3,430 earthworm specimens by the US Bureau of Plant Quarantine over a 15-year period. Often details of full distributional ranges are speculative and more questions are raised than answers—for several earthworm species even their place of origin is obscured by frequent transportations. Thus, much scope exists for further ecotaxonomic survey to help understand and explain the origins and dispersal mechanisms of cosmo-

politan earthworm species, and perhaps the use of molecular analyses of types will help provide answers to fill some of the many gaps in our knowledge.

14.8 BENEFITS AND RISKS OF EARTHWORM TRANSPORTATIONS

Earthworms are reported to sometimes be deliberately transported, e.g. Australian natives from Mt. Kosciusko were exported to the Scottish Cairngorms in an attempt to reduce peat turf mats there (Sims and Gerard 1985, 1999), and a worldwide trade in vermicomposting and fishing bait worms exists. Naturally, a specimen's attendant parasites, pathogens and symbionts accompany it in its travels. Imposition of quarantine barriers and awareness of invasive species problems help regulate such dispersion and, although earthworms are usually considered beneficial or benign, some risk assessment is required as some deleterious effects have emerged (e.g. Hendrix and Bohlen 2002). Examples of environmental risk include exotics *E. saltensis* (Beddard 1895) from South America and recently discovered in Japan (Blakemore et al. 2007), which is considered a pest in Australian rice paddies (Stevens and Warren 2000), and *Dichogaster annae* (Horst 1893), reported as its junior synonym *Dichogaster curgensis* Michaelsen 1921, which is indicated as a serious pest of rice terraces in the Philippine Cordilleras (Barrion and Listinger 1997). Other invasives in lowland tropics are *P. corethrurus* and the *P. elongata* species complex, both of which tend to dominate the native faunas and have some negative agroecological reports (e.g. Stephenson 1930; Gates 1972; Rose and Wood 1980; Blakemore 1994, 1997, 2002, 2006a). Gates (1972) noted that *P. corethrurus*, along with *Po. elongata* (15.6% of the earthworm population), was implicated in rendering a South Indian soil cloddy and unproductive (Puttarudriah and Sastry 1961). Seepages from taro patches on Kauai, Hawaii, from rice paddies in Taiwan and from the famous 2,000-year-old mountain terraces of Ifugao, Philippines were all attributed to morphs identified by Gates as *P. elongata* (see also Joshi et al. 2000). Nevertheless, benefits are also reported (e.g. Spain et al. 1992) and feeding experiments showed Papuan pigs to have a preference for *P. corethrurus* compared with for native species (Sims and Gerard 1999); also, apparent plant growth enhancement has been observed through the activity of this species (Fig. 14.3).

Overwhelmingly, studies show increased plant productivity when earthworms are deliberately added to the soil or when they are encouraged by improved soil management

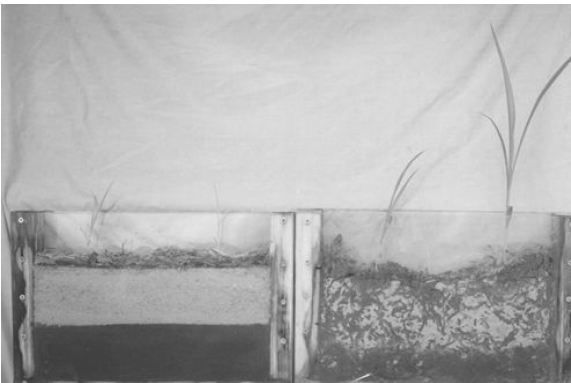


Figure 14.3 Demonstration of effect of adding earthworms (*Pontoscolex corethrurus*) on soil and litter layers, and plant (*Sorghum bicolor*) growth after 2 weeks: lhs = no worms; rhs + five worms.

Source: Photo courtesy of Dr. Les Robertson. (See color insert.)

(Lee 1985; Brown et al. 1999; Blakemore 2002, 2006a). Whether exotic species compete with or displace natives is debatable, although Lee (1987) stated, “There is no documented case of direct competition between previously established and newly introduced earthworms.” The examples given by Lee (1987) seem to support conclusions by Wood (1974) and Kalisz and Wood (1995) that natives living superficially (but not necessarily subsoil species) mainly decline when natural vegetation is replaced with cultivated vegetation, rather than through direct competition with introduced earthworm species. Moreover, some indigenous earthworms may be more adaptable and persistent under cultivation than is generally realized, as shown by a few reports from ecotaxonomic studies (e.g. Lavelle 1978; Abbott et al. 1985; Blakemore 1994, 1997a; Blakemore and Elton 1994; Blakemore and Paoletti 2007).

14.9 CONCLUSIONS

According to Grayson (2001), “It now appears extremely unlikely that there are any habitable places on earth whose terrestrial biotas were not structured by prehistoric human activities.” To this we may add that no region is known to lack introduced earthworms for similar reasons. Earthworms often have remarkably high biodiversity, yet routine agroecological studies tend to overemphasize the importance of just the Lumbricidae components rather than consider contributions of natives and nonlumbricid cosmopolitans. This may be due partly to the difficulty for nonspecialists to identify natives (which require dissection for identification) or the smaller exotics that are easily missed or mistaken for immatures, and partly to studies historically concentrating on just Lumbricidae of European origin even when transplanted to new areas such as North America or Australia (e.g. Edwards and Lofty 1977; Edwards and Bohlen 1996). While the natural spread of earthworms can be slow or negligible, the dispersion of exotics appears to closely follow cultural and technological trade and exchanges: gradually in preagricultural societies, more extensively following the Agricultural Revolution, accelerating during the Industrial Era and subject to globalization in the current period. Thus, earthworm transportation is considered to be mainly human mediated with exotic species’ origins often corresponding with provenances of traditional agricultural and horticultural crops.

The compilation and online presentation of earthworm distribution and diversity data is important. Concerted efforts could readily generate a unified checklist of all 6,000 earthworm species, having the most current binomial as the universal identifier under the *International Code of Zoological Nomenclature* (ICZN 1999), with the realization that each species is an ecologically unique entity and that casting light on its origins and peregrinations may help illuminate human history. Ideally, a database matrix should be cross referenced by region (and habitat) to gauge biodiversity and to plot the current or potential spread of exotics and their possible competition with natives, or any unexpected consequences such as acting as intermediate hosts or disease vectors. Earthworms are generally considered beneficial or benign, albeit deleterious environmental effects of some invasive earthworm species have been reported and their environmental risk/benefit needs to be assessed on a case-by-case basis.

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